

A CONTRIBUTION TO THE TAXONOMY OF BORAGINACEAE

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ABSTRACT

Macro-and micro-floral characters of 34 taxa of Boraginaceae were investigated. The data in this work could be both diagnostic and interpretative. An interesting correlation was found to exist between the lobing of the ovary on one hand and the style insertion, the ovule attachment and the fruit type on the other hand. The vascular supply of the perianth leaves and the stamens showed no serious fluctuations. That of the gynoecium showed marked plasticity expressed by amplification through splitting, reduction through missing or fusion, and by diversified feeding of the styles by vascular supply from different origin. Twelve of the recorded characters were chosen as evolutionary dicta for the family, and the discussion of all led to a schematic presentation of presumed intra-affinities. Among the latter, it has been suggested that Heliotropium represents an evolutionary stock from which all other taxa can radiate; and H. digynum with its hexamerous flower may be the core of this genus. Previous opinions on the micro-evolution in the Boraginaceae have been discussed in view of our data.

INTRODUCTION

Phylogenetic treatments of Boraginaceae were rather diverse and an extreme was the isolation by Hutchinson (1948) of a number of its members under an additional family the Ehretiaceae. Impressed by their habit he treated both families as radiating from two evolutionary stems; Boraginaceae from Herbaceae and Ehretiaceae from Lignosae.

Several taxonomists (e.g. Hallier 1912, Bessey 1915, Brand 1921, Wettstein 1935, Johnston 1923-49, Lawrence 1963, Chopra 1971, Takhtajan 1980; and others) have discussed the intra-relations of Boraginaceae taxa as well as its affinity to other families. These discussions led to more or less empirical view-points. Meanwhile the taxonomic treatment of the family main subdivisions might have received less arbitrary arguments: and the Englerian 4 sub-families and 6 tribes have shown themselves to be the classically acceptable major sub-taxa. The limitation of these ranks relied entirely upon the enumerated characters: (i) aspect of the ovary, topography and aspect of the style, and (iii) the fruit type. Coupled with other floral characters all were assertive where used as diagnostic. However, the discipline of floral morphology as an approach to taxonomy began as early as 1871 by Van Tieghem who also raised an attention to the marked variations of styles and stigmas within Heliotropioideae. More recently the same approach as applied to Boraginaceae can be exemplified by the work of Hutchinson (1969), Fabre & Nicoli (1974) Joshi (1975, 76) Di Fulvio (1978), Schmidt (1978) and Khelifa & Hamed (1982).

Here, it would be space-consumption to raise the significance of such an approach although it yielded data that made possible, in many places, rational comprehensions to puzzling matters as character plasticity and correlation, the nature of extra-floral organs, the magnitude of attributes: and the like: thus settling dubious cases in taxonomy and phylogeny. Convinced by this we here are investigating 33 spp. and one variety for more contribution to the taxonomy of Boraginaceae.

MATERIALS AND METHODS

Flower buds of 33 spp. and one variety in 18 genera were studied. The materials were fixed in FAA, embedded in wax, stained in safranin-light green combination and serially cross sectioned at 8-10 μ m according to the conventional methods. The observations were mostly condensed in tabular form. The drawings were deliberately avoided for our observations showed no essential deviation from those previously recorded by other workers. In this paper the taxa in any place are dealt with in the sense of Engler and Prantl. Table I, shows the collection data.

TABLE I. COLLECTION DATA

SUB-FAMILY	TRIBE	SPECIES
I. Ehretioideae		1. <i>Ehretia buxifolia</i> Roxb.*
II. Cordioideae		2. <i>Cordia myxa</i> L.
		3. <i>C. sebestena</i> L.*
		4. <i>C. tremula</i> Griseb.*
III. Heliotropioideae		5. <i>Heliotropium arabinense</i> Fres.
		6. <i>H. bacciferum</i> Forsk.
		7. <i>H. digynum</i> (Forsk.) Asch. ex C. Christens
		8. <i>H. europaeum</i> L.
		9. <i>H. supinum</i> L.
		10. <i>H. sp. 1</i>
		11. <i>H. sp. 2</i> *
IV. Boraginoideae	Cynoglosseae	12. <i>Cynoglossum officinale</i> L.*
		13. <i>Trichodesma africanum</i> (L.) R.Br
	Eritricheae	14. <i>Echiochilon fruticosum</i> Desf.
		15. <i>Lappula deflexa</i> (Lehm.) Grache
	Anchuseae	16. <i>Symphytum tuberosum</i> L.**
		17. <i>Borago officinalis</i> L.**
		18. <i>B. orientalis</i> L.
		19. <i>Anchusa officinalis</i> L.***
		20. <i>A. aegyptiaca</i> (L.) DC.
		21. <i>A. arvensis</i> (L.) M.B.
		22. <i>Alkanna tinctoria</i> (L.) Tausch.
		22. <i>A. t. var. incana</i> Boiss.
		23. <i>Gastroctyle hispida</i> (Forsk.) Bunge
		24. <i>Lycopsis arvensis</i> L.
	Lithospermeae	25. <i>Lithospermum officinale</i> L.**
		26. <i>Arnebia hispidissima</i> (Lehm.) DC.*
		27. <i>Moltikiopsis ciliata</i> (Forsk.) Johns
	Echieae	28. <i>Echium rosulatum</i>
		29. <i>E. creticum</i> L.
		30. <i>E. longifolium</i> Del.
		31. <i>E. sericeum</i> Vahl
	Ceritheae	32. <i>Cerithe minor</i> L.**
		33. <i>C. glabra</i> Mill

Non-asterisked spp. are among the Egyptian flora

* Horticultural spp. in the Faculty Gardens

** Loaned as fixed flower buds

*** Loaned as seeds and raised under the mesophytic conditions

OBSERVATIONS AND DISCUSSION

BILATERAL SYMMETRY

The bilateral symmetry of the corolla in some spp. besides its marked expression in certain Echium spp. promoted Lawrence (1937) to favour its adoption to the tribal limitation. However an earlier view by Johnston (1923-49) restricted it to specific limitation on account of its occurrence in other genera not closely related to Echium. We here support the latter opinion since Echiochilon fruticosum (Eritricheae) is highly zygomorphic.

COROLLA APPENDAGES (TABLE 2)

Puri (1951) reported on their occurrence in a number of families including our's. Here the appendages at the corolla throat (also termed petaloid scales, corona) occur in 13 taxa all in Boraginoideae. Lawrence (1937) gave them value for generic limitation. However their nature would be discussed elsewhere in this paper.

LOBING OF THE OVARY (TABLE 3)

Ovary entire (unlobed) in Ehretia buxifolia and the 3 Cordia spp. Slightly lobed in 8 taxa. Prominently lobed in 5 taxa. Lobed and winged in 7 taxa (with wing-like parenchymatous tissue between the carpels). Lobed and ringed in 10 taxa (with ring-like parenchymatous tissue that persists between the nutlets).

INSERTION OF THE STYLE (TABLE 3)

AND THE NATURE OF THE GYNOBASE

The style is terminal in Ehretia buxifolia, the 3 Cordia spp. and the 7 Heliotropium spp: all with either entire or slightly lobed ovaries. It is gynobasic in 23 taxa with prominently lobed ovaries. Thus we may refer to a correlation between the lobing of the ovary and the topography of the style: the former also determines the fruit type (see next item). However it is observed that the deeper the constriction in the ovary is the lower will be the attachment of the style to the carpels and the more is the tendency towards nutlet formation.

The term "gynobase" has not yet been fully understood although its use dates back in earlier literature (Lawrence 1937). As to its nature Moore (1936 b), considered it as fused staminodes in certain Leguminosae, and as carpelodes in many Apocynaceae. In certain Boraginaceae (Mertensia) the same author (1936a) interpreted it as carpelodes. Still in Boraginaceae Joshi (1957) showed that it consists of parenchymatous tissue continuous with the receptacle, and concluded that it can be designated, in part, as placenta. The conclusion of Joshi is in accord with that of Lawrence: that the gynobase is of placental nature since it shares in the body to which the ovules are attached. The present observations show that in taxa with gynobasic

TABLE 2. MACROMORPHOLOGY OF CALYX AND COROLLA

	CALYX				COROLLA		THROAT(SC)	SYMMETRY
	NUMBER	TEXTURE	NUMBER	TEXTURE	LIMB	BASE(PP)		
1. <i>Alkanna tinctoria</i>	5	P	5	G	0	10	+	+
2. <i>A. t. var. incana</i>	5	RH	5	G	0	10	+	+
3. <i>Anchusa aegyptiaca</i>	5	DH	5	G	0	-	+	+
4. <i>A. arvensis</i>	5	RH	5	G	0	-	+	+
5. <i>A. officinalis</i>	5	H	5	G	0	-	+	+
6. <i>Arnebia hispidissima</i>	5	HI	5	G	0	10	-	+
7. <i>Borago officinalis</i>	5	DH	5	G	A	-	+	+
8. <i>B. orientalis</i>	5	R	5	G	A	-	+	+
9. <i>Cerinthe glabra</i>	5	H	5	G	A	10	-	+
10. <i>C. minor</i>	5	H	5	G	A	10	-	+
11. <i>Cordia myxa</i>	6	G	5/6	G	A	5	-	+
12. <i>C. sebestena</i>	2-5	L	12	G	A	-	-	+
13. <i>C. tremula</i>	5/6	L	5/6	G	0	5	-	+
14. <i>Cynoglossum officinale</i>	5	R	5	G	A/0	10	+	+
15. <i>Echiochilon fruticosum</i>	5	RD	5	H	A	-	-	-
16. <i>Echium creticum</i>	5	G	5	H	A	-	-	-
17. <i>E. longifolium</i>	5	H	5	G	A	-	-	-
18. <i>E. rosulatum</i>	5	H	5	H	A	-	-	-
19. <i>E. sericeum</i>	5	H	5	G	0	-	-	-
20. <i>Ehretia buxifolia</i>	4	G	5	H	0	-	+	+
21. <i>Gastroctyle hispida</i>	5	H	5	G	0	-	-	+
22. <i>Heliotropium arabinense</i>	5	R	5	H	A/0	-	-	+
23. <i>H. bacciferum</i>	5	R	5	H	0	-	-	+
24. <i>H. digynum</i>	5/6	R	5/6	G	RE	-	-	+
25. <i>H. europaeum</i>	5	DH	5	H	0	-	-	+
26. <i>H. supinum</i>	5	R	5	H	0	-	-	+
27. <i>H. sp. 1</i>	5	G	5	G	A	-	-	+
28. <i>H. sp. 2</i>	4/5	H	4/5	H	0	-	-	+
29. <i>Lappula deflexa</i>	5	H	5	G	0	-	+	+
30. <i>Lithospermum officinale</i>	5	H	5	G	W	10	+	+
31. <i>Lycopsis arvensis</i>	5	H	5	G	0	-	+	+
32. <i>Moltikiopsis ciliata</i>	5	HS	5	H	A	-	-	+
33. <i>Symphytum tuberosum</i>	5	H	5	G	RE	5	+	+
34. <i>Trichodesma africanum</i>	5	H	5	G	A	-	-	+

A, ACUTE; DH, DENSELY HAIRY; G, GLABROUS; H, HAIRY; HI, HISPID STRIGOSE; L, LEATHERY; O, OBTUSE; P, PUBESCENT; PP, PARENCHYMATOUS PROTUBERANCE; R, RUGOSE; RD, ROUGH DOTTED; RE, REFLEXED; RH, ROUGH HAIRY; SC, SCALES.

styles the ring structure [see previous item] appears likely to be a parenchymatous continuation of the receptacular core thus justifying a composite nature to the gynobase. This structure is built at its base from receptacular tissue and at its sides and top from the inrolled carpellary leaves.

Another correlation can be said to exist between the style insertion and the ovule attachment. In the spp. with terminal styles the ovules become attached at a relatively high level appearing pendulous. As the stylar attachment becomes progressively lowered the ovule attachment is likewise lowered and a climax is reached in the spp. with basal styles where the ovules appear basal, erect and long funicled. Structurally this latter correlation may support the view that the basal part of the style adnate to the ring structure is almost related to placental tissue. Moreover this positive correlation can be signified in Boraginaceae if we think about a functional adaptation of an ovule behaving as a satellite to the style to cut short the road to a successful copulation.

THE FRUIT (TABLE 3)

Nutlet in 22 taxa where the carpels separate from each other with the style inserted in between. Simple nutlet (druplet) in the 7 Heliotropium spp. and in Trichodesma africanum. Drupe in Ehretia buxifolia and the 3 Cordia spp.

Several taxonomists adopted the fruit type as a lead to the sub-families limitation. Thus Cordioideae had been assumed to be primitive on the bases of their entire ovaries maturing into drupes. Ehretioideae and Heliotropioideae with either entire or slightly lobed ovaries have druplets (simple nutlets) and were considered more advanced. Stepping like-wise we may rank Boraginoideae higher for the well developed 4 nutlets its members have in response to the deep lobing of the ovary. However it may be worthy to point out that: (i) Cynoglossum officinale with typical nutlets and Trichodesma africanum with simple nutlets are retained in one tribe Cynoglosseae. (ii) The typical drupe of Ehretia buxifolia stamps it primitive in Ehretioideae although the latter includes other spp. with simple nutlets. (iii) The Heliotropioideae spp. show various degrees of carpellary lobing; thus Heliotropium may be localized between the less advanced Cordioideae (entire ovaries) and the more advanced Boraginoideae (deeply lobed ovaries).

External evidence in favour of the significance of the fruit type at various levels is adopted from Lawrence (1937), Riedl (1967) Fabre & Nicoli (1974) and Schmida (1978). Lawrence (1937) showed that Boraginoideae includes both simple and typical nutlets and Lithospermeae as well as Eritricheae contain some spp. with simple nutlets although winged and ringed types do occur. Fabre & Nicoli (1974) have found that the external morphology of the achene in certain Boraginaceae is of a considerable weight in generic and specific limitation. Earlier to that Riedl (1967) followed the fruit type to separate Paracaryum (with incurved wings) and Mattiastrum (with flattened

TABLE 3. MACROMORPHOLOGY OF ANDROECIUM, GYNOCIDIUM AND FRUIT

	STAMENS NUMBER	ADNATION	GYNOCIDIUM ASPECT	STYLE	STIGMA	FRUIT	
						TYPE	NO. OF D.F.U.
1. <i>Alkanna tinctoria</i>	5	1/4T	L.W	B	S	N	2,4
2. <i>A. t. var. incana</i>	5	2/3T	L.W	B	S	N	1*
3. <i>Anchusa aegyptiaca</i>	5	1/2T	L	B	2L	N	4
4. <i>A. arvensis</i>	5	V	L	B	2L	N	4U
5. <i>A. officinalis</i>	5	V	L.W	B	+F	N	3
6. <i>Arnebia hispidissima</i>	5	AT	L.W	B	2L	N	4
7. <i>Borago officinalis</i>	5	AT	L	B	S	N	4
8. <i>B. orientalis</i>	5	AT	L.W	B	S	N	4U
9. <i>Cerinthe glabra</i>	5	1/2T	L.W	B	S	N	4
10. <i>C. minor</i>	5	1/2T	L.W	B	+2F	N	4
11. <i>Cordia myxa</i>	6	AT	UL	TE	4F	D	S
12. <i>C. sebestena</i>	13	AT	UL	TE	4F	D	S
13. <i>C. tremula</i>	5,6	1/3T	UL	TE	4F	D	S
14. <i>Cynoglossum officinale</i>	5	1/2T	L.R	B	S	N	2
15. <i>Echiochilon fruticosum</i>	5	1/2T	L.R	B	2F	N	4
16. <i>Echium creticum</i>	5	1/2T	L.R	B	2FI	N	4
17. <i>E. longifolium</i>	5	1/2T	L.R	B	2FI	N	4
18. <i>E. rosulatum</i>	5	1/2T	L.R	B	2FI	N	4
19. <i>E. sericeum</i>	5	1/3T	L.R	B	2FI	N	4
20. <i>Ehretia buxifolia</i>	5	1/3T	UL	TE	2F	D	S
21. <i>Gastroctyle hispida</i>	5	1/2T	L.R	B	S	N	2
22. <i>Heliotropium arabinense</i>	5	1/2T	SL	TE	S	SN	4,2
23. <i>H. bacciferum</i>	5	1/2T	SL	TE	S	SN	4
24. <i>H. digynum</i>	5,6	3/4T	SL	TE	2L	SN	4
25. <i>H. europaeum</i>	5	3/4T	SL	TE	S	SN	4
26. <i>H. supinum</i>	5	1/3T	SL	TE	S	SN	1*
27. <i>H. sp. 1</i>	5	1/3T	SL	TE	S	SN	4
28. <i>H. sp. 2</i>	4,5	1/3T	SL	TE	S	SN	4
29. <i>Lappula deflexa</i>	5	1/2T	L.R	B	2FI	N	4
30. <i>Lithospermum officinale</i>	5	1/3T	L.R	B	S	N	3
31. <i>Lycopsis arvensis</i>	5	2/3T	L	B	2L	N	4
32. <i>Moltikiopsis ciliata</i>	5	3/4T	L	B	+2FI	N	4
33. <i>Symphytum tuberosum</i>	5	3/4T	L.R	B	S	N	4
34. <i>Trichodesma africanum</i>	5	3/4T	SL	+B	S	SN	4

* NUTLETS REDUCED TO ONE BY ABORTION

AT, ALONG THE LENGTH OF THE COROLLA TUBE; B, BASAL; D, DRUPE.
 D.F.U, DEVELOPING FRUIT UNITS, F, FORKED FI, FID : L, LOBED; N, NUTLET;
 R, RINGED. S, SINGLE. SL, SLIGHTLY LOBED; SN, SIMPLE NUTLET;
 T, COROLLA TUBE; TE, TERMINAL. U, UNEQUAL; UL, UNLOBED;
 V, VARIABLE W, WINGED.

wings) Contrary to that Schmida (1978) stated that such separation which is based on this character alone is hardly useful on account of the occurrence of forms with incurved and flattened fruit wings in the different spp. of the same genus viz. Paracaryum intermedium and P. boissieri.

SEPAL VASCULATURE (TABLE 4)

The sepal is supplied with 3 traces: one median and two lateral. The traces behave differently as follows:

1. All differentiate independant in the receptacle from the central stele (Cordia tremula).
2. Median traces branch in the sepals giving the laterals.
3. Median traces arise from a lower set of 5 bundles; and the lateral traces from an upper set of other 5 bundles. Each of the latter branches into two to two adjacent sepals (Heliotropium bacciferum).

PETAL VASCULATURE (TABLE 4)

Amplification in the petal supply is recorded when the petal laterals differentiate from the corolla tube at points just below the separation of the staminal filaments. This observation embodies the 6-merous type of Heliotropium digynum, the 4-merous type of H. sp. 2 and in forms with variable numbers of corolla lobes (Cordia sebestena).

VASCULATURE OF THE COROLLA APENDAGES (TABLE 4)

Two types of such appendages are met with. Those at the base of the corolla tube termed parenchymatous "protuberances", which are not vascularized; and those occurring at the corolla throat either vascularized or not. Our discussion is focussed on those at the throat and 3 types of vasculature are recorded:

1. Appendages without vascular supply (Alkanna tinctoria var. incana, Anchusa arvensis).
2. Appendages with one vascular trace (Anchusa officinalis Lithospermum officinale, Symphytum tuberosum).
3. Appendages with 2 vascular traces (Alkanna tinctoria, Anchusa aegyptiaca, 2 Borago spp., Cynoglossum officinale, Gastroctyle hispida, Lappula deflexa, Lycopsis arvensis).

In this type the appendages are relatively expanded almost at the centre and the traces fuse towards the terminal narrow portion.

TABLE 4. VASCULARIZATION OF SEPAL, PETAL APPENDAGES AND STAMENS

	SEPAL TRACES	APPENDAGE TRACES	SEPARATION OF STAMINAL TRACES
1. <u>alkanna tinctoria</u> , Type (1)	5	2F	B TH
1. -----, Type (2)	5	2F	B TH
2. ----- var. <u>incana</u>	5	NV	B TH
3. <u>Anchusa aegyptiaca</u>	5	2F	B TH
4. <u>A. arvensis</u>	5	NV	TH
5. <u>A. officinalis</u>	5	1	B TH
6. <u>Arnebia hispidissima</u>	5	-	B TH
7. <u>Borago officinalis</u>	5	2F	B TH
8. <u>B. orientalis</u>	5	2F	B TH
9. <u>Cerinthe glabra</u>	5	-	B TH
10. <u>C. minor</u>	5	-	B TH
11. <u>Cordia myxa</u>	N	-	B TH
12. <u>C. sebestena</u>	N	-	M T
13. <u>C. tremula</u> Type (1)	15	-	TH
13. ----- Type (2)	15	-	TH
14. <u>Cynoglossum officinale</u>	5	2F	B TH
15. <u>Echiochilon fruticosum</u>	5	-	TH
16. <u>Echium creticum</u>	5	-	B TH
17. <u>E. longifolium</u>	5	-	B TH
18. <u>E. rosulatum</u>	5	-	TH
19. <u>E. sericeum</u>	5	-	B TH
20. <u>Ehretia buxifolia</u>	N	-	B TH
21. <u>Gastroctyle hispida</u>	5	2F	B TH
22. <u>Heliotropium arabinense</u>	5	-	M T
23. <u>H. bacciferum</u>	10	-	M T
24. <u>H. digynum</u>	5.6	-	TH
25. <u>H. europaeum</u>	5	-	TH
26. <u>H. supinum</u>	5	-	1/3 T
27. <u>H. sp. (1)</u>	5	-	1/3 T
28. <u>H. sp. (2)</u>	4.5	-	M T
29. <u>Lappula deflexa</u>	5	2F	B T
30. <u>Lithospermum officinale</u>	5	1	B T
31. <u>Lycopsis arvensis</u>	5	2F	B TH
32. <u>Moltikiopsis ciliata</u>	5	-	M T
33. <u>Symphytum tuberosum</u>	5	1	M T
34. <u>Trichodesma africanum</u>	5	-	M T

-, APPENDAGE ABSENT; BT, BASE OF COROLLA TUBE; B TH, BASE OF COROLLA THROAT; F, FUSED; MT, MIDDLE OF COROLLA TUBE; N, NUMEROUS; NV, NON-VASCULARIZED; T, COROLLA TUBE; TH, COROLLA THROAT.

As to their nature Schleiden (1849) identified a scale as merely an elaborated fold representing dependant appendage of the foliar organ developing originally simple and flat. Gurke (in Engler & Prantl 1897) looked to the scales as a ring of abortive stamens. Lawrence (1937) regardless of its topography, considered the scale to be a fold of the corolla tissue. Joshi (1975) did not comment on their nature although he gave them a generic value in Boraginaceae.

The variability of vasculature as recorded in this work would encourage the refutation of Gurke's staminal concept about the nature of the scales; a refutation further confirmed by their vascular supply which comes from the petal traces. In accordance with Lawrence we would assert upon the corollary folding nature of the scales at the corolla throat. We may add; the degree of folding would determine the number of traces; either one in less expanded or 2 in relatively expanded scales.

STAMEN VASCULATURE (TABLE 4)

Five alternate staminal traces diverge close to and above the petal traces, tress-pass the corolla tube and eventually enter the filaments when the latter become free. The separation of the stamens from the corolla tube takes place at different levels in the different taxa.

GYNOCIDIUM VASCULATURE (TABLE 5)

In all taxa the ovary is 2-carpelled, 4-loculed with a single ovule in each. Normally the carpel is a 3-trace organ. However the following vascularization patterns were recorded:

1. Dorsal bundles: Absent altogether in Cordia tremula, Ehretia buxifolia and Gastroctyle hispida. In Alkanna tinctoria (Type 1) only one bundle was recorded; and in this sp. a reduction of half of the ovary resulted in the formation of 2 simple nutlets. In Heliotropium spp. [except H. sp. 2] 4 bundles were recorded. The remainder taxa had 2 bundles each; one for each carpel.

As to their behaviour:

Type (a): Normal (unchanged). In 22 taxa; where each carpel has its dorsal which passes inward and upward to the top of the nutlet, then passes inward to run into the style. The 2 dorsals give laterals to supply the periphery of the carpels.

Type (b): Fused. In Heliotropium arabinense, H. europaeum and H. supinum 4 dorsals are present, 2 to each carpel Each pair fuses at the top of the ovary to run into the style.

Type (c): Splitted. In Cordia sebestena where the 2 dorsals of the 2 carpels split into 4 before entering in the style.

Type (d): Fading. In Heliotropium digynum and H. sp. 1; where 4 dorsals are ill-developed and fade out near the summit of the ovary. The stylar supply comes from the 4 septal bundles. In Heliotropium sp. 2 each carpel

is supplied with one dorsal which fades at the base of the ovary.

2. Ventral bundles: Four were observed to represent the ovular supply. However only 2 were recorded in Type 2 of *Alkanna tinctoria* and in *Ehretia buxifolia* where the ovary is 2-loculed, 2-ovuled. As to their behaviour Lawrence (1937) pointed out that one would expect the occurrence of 4 ventrals in the lowest forms of the family; each giving one ovular trace, and they all would continue to the top of the ovary. However, the following behaviour has been recorded.

Type (a): Normal in 29 taxa where the 4 ventrals give the ovular supply then fade at once. This is common in Boraginoideae and confirms Lawrence (1937). However similar behaviour has been on record in the other sub-families.

Type (b): Splitted. In *Cordia myxa* the number is increased through splitting of the 4 ventrals into 6 traces: 4 of the latter supply the ovules then extend into the style. In *Ehretia buxifolia* the 2 ventrals split into 4 traces to supply the ovules; then fuse to form the styler supply. In this connection Lawrence (1937) mentioned that in *Cordia cumingiana* and *Ehretia viscose* the fused bundles continue to the top of the ovary and fuse with the laterals. In *cordia alliodora* and *Ehretia canariensis* the ventral bundles fade out below the top of the ovary. Thus two evolutionary trends had been assumed to occur in sub-families Cordioideae and Ehretioideae. The same author added that the cases in which the ventral bundles continue to the top of the ovary (after supplying the ovules) would be expected to represent the lowest forms of the Boraginaceae. More recently Joshi (1976) recorded similar behaviour of ventrals in *Cordia dichotoma*, *C. gharal* and *Ehretia aspera*.

Type (c): Fused. In *Cordia tremula* and *Gastroctyle hispida* in which, after supplying the ovules, the 4 ventrals fuse into 2 to feed the style. The occurrence in *Gastroctyle hispida* of such behaviour is not unexpected since the carpellary dorsals are wanting and this might be a primitive case among the Boraginoideae. Meanwhile its occurrence in *Heliotropium* spp. might be attributed to the reduction of the 4 dorsals to 2 besides the missing of the 4 septals in other spp. of this genus. In *Heliotropium* sp. 2 the continuation of the ventrals after supplying the ovules might be a transitional case within this genus.

THE STYLAR SUPPLY (TABLE 5)

1. Derived from the 2 carpellary dorsals (in 24 taxa).
2. Derived from the 2 carpellary ventrals in *Cordia tremula*, *Ehretia buxifolia* and *Gastroctyle hispida*: where the 2 ventrals are a fusion product of 4 bundles.
3. Derived from one ventral and one dorsal. In *Alkanna tinctoria* (Type 1) having 2 locules with one ovule in each. The dorsal trace is one and the ventral traces are 2. The latter traces branch beyond the ovular supply and move inward to enter a columnar tissue. Then a trace from this tissue opposite the dorsal and together with it forms the styler supply.

NECTARY
DISC
COLUMNAR
TISSUE
STYLAR
SUPPLY
BEHAVIOUR
OF V.B.
BEHAVIOUR
OF D.B.
SEPTAL
BUNDLES(S.B.)
VENTRAL
BUNDLES(V.B.)
DORSAL
BUNDLES(D.B.)

1. <u>Alkanna tinctoria</u> Type 1	2	4	2	N	F	IV.B+1D.B	+	-
1. ----- Type 2	2	4	2	N	N	2D.B	+	-
2. ----- var. <u>incana</u>	2	4	W	N	N	2D.B	+	-
3. <u>Anchusa aegyptiaca</u>	2	4	W	N	N	2D.B	-	+
4. <u>A. arvensis</u>	2	4	W	N	N	2D.B	+	+
5. <u>A. officinalis</u>	2	4	W	N	N	2D.B	+	+
6. <u>Arnebia hispidissima</u>	2	4	W	N	N	2D.B	+	+
7. <u>Borago officinalis</u>	2	4	W	N	N	2D.B	+	+
8. <u>B. orientalis</u>	2	4	W	N	N	2D.B	+	+
9. <u>Cerithe glabra</u>	2	4	2	N	N	2D.B+2S.B	-	+
10. <u>C. minor</u>	2	4	W	N	N	2D.B	+	+
11. <u>Cordia myxa</u>	2	4	W	FA	SP	4V.B	+	+
12. <u>C. sebestena</u>	2	4	2	SP	N	4D.B	+	+
13. <u>C. tremula</u> Type 1	W	4	W	W	F	2V.B	+	+
14. ----- Type 2	W	4	W	W	F	2V.B	+	+
15. <u>Cynoglossum officinale</u>	2	4	W	N	N	2D.B	+	+
16. <u>Echiochilon fruticosum</u>	2	4	W	N	N	2D.B	+	-
17. <u>Echium creticum</u>	2	4	W	N	N	2D.B	+	-
18. <u>E. longifolium</u>	2	4	W	N	N	2D.B	-	-
19. <u>E. rosulatum</u>	2	4	W	N	N	2D.B	+	-
20. <u>E. sericeum</u>	2	4	W	N	N	2D.B	+	+
21. <u>Ehretia buxifolia</u>	W	2	W	W	SP	4V.B	+	+
22. <u>Gastroctyle hispida</u>	W	4	W	W	F	2V.B	+	+
23. <u>Heliotropium arabinense</u>	4	4	4	F	N	2D.B	-	+
24. <u>H. bacciferum</u>	4	4	4	FA	N	4S.B	-	+
25. <u>H. digynum</u>	4	4	4	FA	N	4S.B	-	+
26. <u>H. europaeum</u>	4	4	4	F	N	2D.B	+	-
27. <u>H. supinum</u>	4	4	4	F	N	2D.B	+	+
28. <u>H. sp. 1</u>	4	4	4	FA	N	4S.B	+	-
29. <u>H. sp. 2</u>	2	4	W	FA	F	4V.B	-	-
30. <u>Lappula deflexa</u>	2	4	W	N	N	2D.B	-	-
31. <u>Lithospermum officinale</u>	2	4	W	N	N	2D.B	-	-
32. <u>Lycopsis arvensis</u>	2	4	W	N	N	2D.B	+	-
33. <u>Moltikiopsis ciliata</u>	2	4	W	N	N	2D.B	+	-
34. <u>Symphytum tuberosum</u>	2	4	W	N	N	2D.B	-	-
35. <u>Trichodesma africanum</u>	2	4	W	N	N	2D.B	+	-

-, ABSENT; F. FUSED; FA. FADING; N. NORMAL; +, PRESENT; SP, SPLITTING; W. WANTING.

THE COLUMNAR TISSUE (TABLE 5)

Present in 24 taxa. It is an extension of the pith from the receptacle upwards to the level where the carpellary laterals differentiate.

THE NECTARY DISC (TABLE 5)

Well developed in 18 taxa. In *Heliotropioideae* it is represented by the swollen bases of the ovaries. As to its nature the disc may be receptacular or carpellary depending on the behaviour of the carpellary dorsals.

1. Receptacular: Here the dorsals differentiate above the disc structure (*Cordia tremula* and *Ehretia buxifolia*).
2. Carpellary: When the dorsals differentiate below the disc (*Anchusa* spp., *Arnebia hispidissima*, *Borago* spp., *Cerinthe* spp., *Cynoglossum officinale*, *Heliotropium arabinense*, and *H. bacciferum*). In other taxa (*Cordia myxa*, *C. sebestena*, *Echium sericeum*, *Heliotropium digynum* and *H. supinum*) we could not rule out its nature and such cases might be inbetween.

CONCLUDING REMARKS

The subsequent remarks represent a cumulative consideration of the floral characters that might be significant to the taxonomy of *Boraginaceae*: both diagnostic and interpretative.

1. NUMBER OF THE PERIANTH LEAVES

Multi-directional relations inside a family may be comprehended when the ancestor is postulated to have a flower with inconsistent number of perianth leaves. In general 6-merous flowers show an inherent plasticity when other types are to be derived. In *Boraginaceae sensu lato* pentamery is the rule. However 6-merous flowers have been recorded in certain spp. of *Cordia*, *Ehretia* and *Heliotropium*. In the latter genus 4-mery occur as well.

Primitive forms of *Boraginaceae* have long been accepted to be the *Cordioideae* and the *Ehretioideae*. In both 5-mery is not the rule. Here it could be suggested that *Heliotropium digynum* may be related to the 6-merous taxa of both sub-families. Meanwhile 4-mery in certain spp. of this genus may be derived from 5-merous flowers through the loss of one set as an evolutionary trend.

2. THE COROLLA APPENDAGES

Our observations show that, unlike those on the base, the appendages on the throat are apparently of more taxonomic significance. The basal scales, if any, could be considered as mere superficial folds of the corolla tissue since they are always not vascularized. Meanwhile vascularization (when present) of the appendages on the throat is assumed to be correlated

with folding of the corolla tissue and the number of vascular bundles in each is determined by the degree of their expansion.

3. LOBING OF THE OVARY AND THE FRUIT TYPE

The lobing of the ovary determines nutlet formation and it is primarily on this that the sub-families have been given their relative position. A primitive case is assumed to be in Cordia spp. and in Ehretia buxifolia since the carpels are entire and mature into a drupe. In other taxa the moderate lobing leads to the formation of simple nutlets (druplets); and full lobing leads to the more advanced typical nutlets characteristic of the family. The progressive lobing starts from slight to winged to the more advanced ringed form. In this connection a transitional aspect is observed in the 7 Heliotropium spp. studied; and this together with floral symmetry may substantiate an intermediate evolutionary status of this genus.

4. STYLE INSERTION AND OVULE ATTACHMENT

It has been observed that the deeper the furrowing into the sides of the carpels is the lower is the attachment of the style. Slightly furrowed ovaries (Cordia spp., Ehretia buxifolia and Heliotropium spp.) have terminal (or lateral) styles. In some taxa deep furrowing results in entire separation of the style to be borne on the gynobase. Likewise; the ovule attachment seems to be affected by the style insertion; appearing apical with terminal styles and basal with gynobasic styles.

5. STIGMA

In most systems the stigmatic modification is the lead character to separate Heliotropioideae and Ehretioideae. Evolutionary the dictum "from many to few" would make the single (entire) stigma an advance over the lobed, fid and forked forms. In the present study most taxa of sub-family Boraginoideae have the single stigma. Within Heliotropioideae, Heliotropium digynum is likely representing a less advanced case in this genus for its bilobed stigma.

6. CALYX, COROLLA AND ANDROECIUM VASCULATURE

The 5-merous flower represents a common pattern with 3-trace sepal, one trace petal and one trace stamen. In all cases the stamens are fused with the petals to a considerable distance. This plan is not basically changed on the occasional occurrence of 4-merous or 6-merous types. In the two latter cases it was only the number of vascular traces that was either decreased to 4 or increased to 6.

7. GYNOCERIUM VASCULATURE

Following the departure of the stamen traces almost all the remaining vascular tissue incorporates in the supply of the carpels and their adherent structures. Various patterns of vasculature of the ovary, the ovules and the styles have been observed, but the most significant of all are, perhaps,

those of the styles. In general, the diversity in the number and manner of feeding by the dorsal, ventral, septal and carpellary wall bundles can refer to some taxonomic relationships or evolutionary trends. The latter seem likely to take place within each taxonomic group down to the generic level as in *Heliotropium*. However, the main differences in gynoecium vasculature are demonstrated by variation in the following characters:

- a) Missing of dorsal bundles or carpellary wall bundles.
- b) Amplification through splitting in the number of dorsal or ventral bundles.
- c) Reduction through fusion in the number of dorsal or ventral bundles.
- d) Feeding of the style by different number (2-4) of vascular supplies of either dorsal or ventral; or dorsal and ventral; or septal or dorsal and septal.

8. NECTARIFEROUS DISC

Its nature can be comprehended through the gynoecium vasculature. Thus the disc is considered to be receptacular in taxa where the carpellary dorsal traces differentiate above its tissue. When the same differentiate below the disc, the latter is considered to be of carpellary nature. However, the rapid development of particular regions renders a difficulty to delimit its nature.

In accordance with the current evolutionary dicta the following are suggested for *Boraginaceae* as being primitive vs advanced.

Hexamerous flowers vs pentamerous vs Tetramerous; Actinomorphy vs Zygomorphy; Entire carpels vs Winged vs Ringed; Unfused carpellary walls vs Fused; Nectariferous disc present vs Absent; Terminal style vs Basal style; Forked stigma or fid or lobed vs Single (entire); Apical ovule vs Basal; Drupe vs Druplet vs Nutlet; Carpellary dorsal bundles absent vs present; Free vascular traces vs Fused; Ventral stylar supply vs Septal vs Dorsal.

The application of the above suggested dicta results in constructing some intra-affinities schemed in Fig. 1.

An abstract from this figure shows that:

1. No particular taxon possesses as much of primitive characters to be considered a hypothetical ancestor of the family. However, members of sub-families Ehretioideae and Cordioideae, although having some advanced characters (sensu stricto), appear likely to present the most primitive case among the taxa studied. The hypothetical ancestor of the *Boraginaceae* is to be searched for among the lower forms of Ehretioideae rather than in Cordioideae; the latter shows an advance over the former because of an apparent tendency towards fusion of the carpellary walls.
2. That the *Boraginaceae* as a natural family has been previously cited by Lawrence (1963) who reported that it is formed of closely related groups. Some other taxonomists raised the sub-families to the family rank viz. Cordiaceae, Ehretiaceae and Heliotropiaceae Brand (1921), Johnston

[1923-49] and Lawrence [1937] were of the opinion that the *Boraginaceae* would best be considered as being composed of several sub-families rather than small micro-families. However, our data shows that affinities do exist and the different taxa show some sort of parallel evolution.

3. The limitation of hierarchial status to every species is rather difficult since all the taxa exhibit an amalgam of both advanced and less advanced characters. However, a predominance of certain characteristic feature (s) is generally observed for each taxonomic group.
4. The most variation in evolutionary trends is inherent to genus Heliotropium which may be a link between the primitive taxa of *Ehretioideae* and *Cordioideae*, on the one hand, and those of some advanced *Boraginoideae* on the other hand. In this connection Heliotropium digynum seems to be the core of this genus.

It may also be worthy to mention that a close relation between *Heliotropioideae* and *Ehretioideae* has been assumed by Di Fulvio [1978]. Such relation is based on endosperm development, pollen morphology, floral vasculature and some peculiarities of the ovules and the embryos. He also added that according to these similarities Hutchinson's classification [1948] may be refuted since he segregated the *Ehretioideae* as a separate family (*Ehretiaceae*) under the *Verbenales*.

5. An apparent relation is present between the studied Cordia spp. and those of Cerinthe. Thus it may be assumed that tribe *Cerintheae* represents lower form in sub-family *Boraginoideae*. Also a possible relation is shown to exist between Cerinthe spp. and Gastroctyle hispida (*Anchuseae*). Cosequently the latter species may share a feature characteristic of the lower forms of tribe *Anchuseae*.
6. Sub-families *Boraginoideae* and *Heliotropioideae* can be linked via Tricnodesma africanum (Tribe *Cynoglosseae*) and Heliotropium spp. respectively. Such relation contradicts Hutchinson's view [1969] that group *Heliotripeae* should be given a family status leaving the true *Boraginaceae*.
7. The affinities in Fig. 1 reinforce the views of Willis [1967] that *Echieae* must be correctly separated form *Lithospermeae* on the basis of the high tendency of Echium towards zygomorphy. This disagrees with Johnston's classification of tribes *Echieae* and *Cerintheae* under *Lithospeermeae*.
8. The feeding of the style by septal and dorsal bundles is a characteristic features in Cerinthe glabra. On the other hand the stylar supply in *Lithospermeae* comes from dorsal bundles only. This may disagree with the view of Willis [1967] that Cerinthe would be a genus related to tribe *Lithospermeae* rather than being considered as a separate group. In spite of this, our suggestion to isolate Cerinthe as an independant genus agrees with the views of other authors [Post, 1932].

9. Our proposed relations between the tribes of Boraginoideae much agree with postulations of Johnston and Lawrence that the Anchuseae and Eritricheae have been derived from Lithospermeae and the Cynoglosseae from Lithospermeae through Eritricheae. The same authors also assumed that tribe Anchuseae might be separated as an off-shoot of Lithospermeae.

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